DOI:
10.1037/neu0000314

Document Version
Peer reviewed version

TO APPEAR IN "NEUROPSYCHOLOGY"
Slow wave and REM sleep deprivation effects on explicit and implicit memory during sleep.

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Abstract Word Count: 248

Text Word Count:8,297

ABSTRACT

Objective: It has been debated whether different stages in the human sleep cycle preferentially mediate the consolidation of explicit and implicit memories, or whether all of the stages in succession are necessary for optimal consolidation. Here we investigated whether the selective deprivation of slow wave sleep (SWS) or rapid eye movement (REM) sleep over an entire night would have a specific effect on consolidation in explicit and implicit memory tasks.

Method: Participants completed a set of explicit and implicit memory tasks at night, prior to sleep. They had one control night of undisturbed sleep and two experimental nights, during which either SWS or REM sleep was selectively deprived across the entire night (sleep conditions counterbalanced across participants). Polysomnography recordings quantified precisely the amount of SWS and REM sleep that occurred during each of the sleep conditions, and spindle counts were recorded. In the morning, participants completed the experimental tasks in the same sequence as the night before.

Results: SWS deprivation disrupted the consolidation of explicit memories for visuospatial information (η^2_p =.23), and both SWS (η^2_p = .53) and REM sleep (η^2_p = .52) deprivation adversely affected explicit verbal recall. Neither SWS nor REM sleep deprivation affected aspects of short-term or working memory, and did not

affect measures of verbal implicit memory. Spindle counts did not correlate significantly with memory performance.

Conclusions: These findings demonstrate the importance of measuring the sleep cycles throughout the entire night, and the contribution of both SWS and REM sleep to memory consolidation.

KEYWORDS

REM sleep; Slow wave sleep; deprivation; memory consolidation

1 INTRODUCTION

There is considerable debate as to whether different sleep stages in the human sleep cycle mediate the consolidation of separate memory processes, or whether all of the stages in the cycle, repeated over the course of the night, are necessary for the optimal consolidation of memory, irrespective of the nature of the learned material (for reviews see Ackermann & Rasch, 2014; Diekelmann & Born, 2010; Diekelman et al., 2009; Oudiette and Paller, 2013; Payne & Nadel, 2004; Rasch & Born, 2013; Walker & Stickgold, 2010).

Many studies have employed the split-night design in which participants undergo only partial deprivation, either early or late in the night (see Fowler, Sullivan, & Ekstrand, 1973; Yaroush, Sullivan, & Ekstrand, 1971). If performance on a task is better after sleep in the first half of the night, relative to sleep in the second half, it is assumed that slow wave sleep (SWS) is more likely to underpin memory consolidation. If performance is better after sleep in the second half of the night, rapid eye movement (REM) sleep is assumed to underlie performance. Studies have shown that SWS-rich, early-night sleep appears to benefit preferentially the consolidation of explicit verbal and spatial memory (e.g., Backhaus et al., 2007; Gais & Born, 2004; Gais, Albouy, Boly, et al., 2007; Plihal & Born, 1997; 1999; Peigneux, Laureys, Fuchs, et al., 2004; Plihal and Born, 1999). Other studies have shown that late-night sleep, dominated by REM, facilitates the consolidation of implicit memory on tasks involving procedural learning, word-stem completion, or perceptual priming (Fischer, Hallschmid, Elsner, & Born, 2002; Maquet, Laureys, Peigneux, et al., 2000; Peigneux et al., 2003; Walker, Brakefield, Morgan, Hobson, & Stickgold, 2002; Walker & Stickgold, 2004; 2006; Plihal & Born, 1999; Wagner, Hallschmid, Verleger, & Born, 2003; Karni,

Tanne, Rubenstein, et al., 1994). Together, these studies posit the dual process hypothesis of memory consolidation during sleep, in which specific sleep stages support the consolidation of different types of memory (see Maquet, 2001); SWS preferentially underpins the consolidation of explicit memory, whereas REM sleep promotes the consolidation of implicit memory.

While it has been claimed (Born & Gais, 2000; Vertes & Eastman, 2000) that the split-night design is advantageous over the deprivation of a sleep stage (or stages) throughout the night, which might induce a stress response, Morgenthaler, Wiesner, Hinze, et al. (2014) found that morning self-evaluations of stress-influenced emotional and arousal states did not differ between selective REM deprivation and undisturbed sleep groups. Similarly, Genzel et al. (2009) found that selective SWS or REM sleep deprivation throughout the night did not affect measures of concentration and stress. Moreover, it is not clear whether a split-night deprivation design is optimal for the study of memory consolidation in sleep. It assumes all early sleep is slow-wave and all late-sleep is REM sleep, and it does not allow precise quantification of each sleep stage across the entire night. Additionally, circadian influences differ across learning and retrieval tasks, and the two conditions in the split-night design may differ in this respect (e.g., Mander, Santhanam, Saletin, & Walker, 2011; Walker, 2008; Walker & Stickgold; 2004; 2006).

Some investigations have produced conflicting findings as to whether observed effects on memory are underpinned by SWS or REM sleep. Some authors have argued that all sleep stages may be involved in aspects of memory consolidation (e.g., Aly & Moscovitch, 2010; Gais, Plihal, Wagner, & Born, 2000; Giuditta, Ambrosini,

Montagnese, et al., 1995). There is evidence that REM sleep preferentially mediates consolidation for memories with a high emotional content (e.g., Nishida, Pearsall, Buckner & Walker, 2009; Wagner, Gais, & Born, 2001; Weisner, Pulst, Krause, et al., 2015), and/or the temporal and spatial components of episodic memories (Rauchs, Bertran, Guillery-Firard, et al., 2004). Others argued that these discrepant findings might result from differences in task difficulty, emotionality, or design (Genzel, Dresler, Wehrle, Grözinger, & Steiger, 2009; Walker & Stickgold, 2005). With respect to implicit memory, Rauchs et al. (2006) did not find any advantage for either SWS or REM sleep on an object priming task, whereas Stickgold and colleagues showed that overnight improvements on a visual texture discrimination task correlated with the overnight quantity of both SWS and REM sleep (Stickgold, James, & Hobson, 2000; Stickgold, Whidbee, Schirmer, et al., 2000). Genzel et al. (2009) found that neither the selective deprivation of SWS nor REM sleep affected the consolidation of explicit (verbal paired associates) or implicit (finger tapping) memories. Instead, they found that sleep spindles (in Stage 2 sleep) appeared to contribute to the consolidation of explicit information (see also Schabus, Gruber, Parapatics, et al., 2004). Others have found that spindle counts are associated with changes in verbal and/or perceptual memory (Westerberg et al 2012; Mednick et al 2013), or with both explicit and implicit learning (Fogel & Smith, 2011; Bodiz, Lazar, & Rigo, 2008; Bakarat et al., 2011).

More recent investigations have examined these issues by employing such techniques as transcranial stimulation during naps (Westerberg, Florzack, Weintraub, et al., 2015); cueing memory reactivation or stimulating sleep specific brain oscillations (Diekelmann, 2014); pharmacological manipulations (Diekelmann, 2014; Mednick,

McDevitt, Walsh, et al., 2013); monitoring spindle density (Mednick et al., 2013; Westerberg, Mander, Florzack, et al., 2012); and recording intracranial EEG activity, or measuring medial prefrontal cortical grey matter volume (Mander, Rao, Lu, et al., 2013; Staresina, Bergmann, Bonneford, et al., 2015). Generally, these techniques have corroborated the findings of many deprivation studies in that there is a link between SWS and memory consolidation, which is attenuated in normal ageing and Mild Cognitive Impairment (Ackerman and Rasch, 2014; Dickelmann, 2014; Mander et al 2013; Westerberg et al., 2012; 2015). However, the putative contributions of REM sleep and spindle density to memory consolidation remain controversial. REM sleep has been associated with perceptual memory (Mednick, Nakayama, & Stickgold, 2003; Mednick et al., 2013), procedural memory (Ackermann and Rasch, 2014), and the stabilisation of consolidated memories (Rasch and Born, 2013).

Consequently, some researchers (Akermann & Rasch, 2014; Stickgold, 2013) have argued that the SWS versus REM sleep account of the dual process hypothesis does not adequately capture the contribution of sleep in memory consolidation. Studies suggesting a contribution of several sleep stages in consolidation have prompted an alternative 'sequential hypothesis' (Diekelmann & Born, 2010; Giuditta et al., 1995; Inostroza & Born, 2013; Stickgold, 2009; Stickgold & Walker, 2007; Walker & Stickgold, 2010). This proposes that sleep optimises the consolidation of a memory when SWS and REM sleep occur in cyclical succession across the night. Sleep stage specificity exists, not for categories of memory (explicit or implicit), but for differing stages in the consolidation process (Stickgold, 2009). According to this view, SWS mediates initial consolidation, and subsequent epochs of REM and Stage 2 sleep facilitate the abstraction and generalisation of information across associated networks

(Landmann, Kuhn, Piosczyk, et al., 2014; Stickgold & Walker, 2007; Walker & Stickgold, 2010).

Attention has turned to another model of sleep-mediated memory consolidation, incorporating elements of both the dual process and sequential hypotheses. As Marr (1971) proposed (cf., Dudai, 2004), memory representations are redistributed between different neuronal systems, from temporary, fast-learning stores (e.g., hippocampus), to slow-learning long-term storage across distributed cortical networks. A new memory is initially encoded in both stores. During consolidation, repeated reactivation of the new memory in the faster learning store drives the simultaneous reactivation in the cortex, such that the memory representation in the cortex is strengthened, and extraction of the invariant properties of the new memory is facilitated. According to the active systems consolidation hypothesis, the reactivation and redistribution of memories occur during sleep in order to prevent interference (Born & Wilhelm, 2012; Dieklemann & Born, 2010; Rasch & Born, 2013). Much of the evidence for this hypothesis comes from studies examining hippocampus-dependent explicit memory, although there is some evidence of systems consolidation for implicit procedural memory consolidation (see Rasch & Born, 2013). According to Born and Wilhelm (2012), newly encoded memories are repeatedly reactivated during SWS, with slow oscillations driving sharp-wave ripples and thalamo-cortical spindles, which, in turn, facilitate the gradual distribution of new memories to long term storage in the cortex. This qualitative reorganisation of the memory representation is thought to be stabilised during consolidation, and is assumed to occur during REM sleep (e.g., Ribeiro, Shi, Englehard, et al., 2007).

In summary, a great deal of evidence exists to suggest a role for SWS in memory consolidation, particularly in the consolidation of explicit memories. However, the role of REM sleep and sleep spindles in memory consolidation remains uncertain, as does the nature by which sleep stages interact over the entire night to facilitate consolidation. Therefore, in this study, we have investigated whether the selective deprivation of either SWS or REM sleep over an entire night would have specific effects on explicit and implicit memory tasks, and/or whether they appear to act in concert. We have quantified the degree of SWS and REM sleep deprivation in each condition. We also took the opportunity to record sleep spindles. By carefully recording sleep stages throughout the night, we tested the hypotheses that:

1. Explicit memory is primarily consolidated during SWS. Therefore, the explicit recollection of visuospatial and verbal information will be poorer following SWS deprivation than after either REM sleep deprivation or a full night of undisrupted sleep.

2. Implicit memory is consolidated during REM sleep. Thus, a greater reduction in visual word priming will be obtained following REM sleep deprivation than after either SWS deprivation or a full night of undisturbed sleep.

3. Attention and working memory would not be affected by specific sleep stage disruption.

2 METHOD

2.1 Participants

Nineteen undergraduates from King's College London were recruited via an email circular; one participant did not complete the protocol, resulting in a final sample size of 18 (9 male). Exclusion criteria were working night-shifts; a diagnosis of sleep disorder; known memory disorder or dysexecutive syndrome or head injury; consumption of 4 caffeinated drinks and/or 5 units of alcohol daily or use of illicit substances; taking prescribed medication with known sedative effects; diagnosis of systemic disorders which might affect sleep pattern; or a body mass index greater than 30. No participants were excluded following screening for psychiatric disorder using the Mini International Neuropsychiatric Interview (Sheehan, Lecrubier, Sheehan, et al., 1998).

Participants were aged between 18 and 35 years (M=23.3, SD=4.3). All were right-handed and spoke English fluently. Participants had completed a mean of 15.6 years of education (SD=1.85). They provided written, informed consent and were reimbursed for their time. Ethical approval was granted by the Joint Research Ethics Committee of the Institute of Psychiatry and South London & Maudsley NHS Foundation Trust (Ref. 05/Q0706/109).

2.2 Design

A repeated-measures, Latin-square design was employed. Independent variables comprised three sleep conditions: a control night of undisturbed sleep, SWS deprivation, and REM sleep deprivation.

2.3 Materials

2.3.1 Cognitive Screening

Background neuropsychological tests were administered to screen for cognitive impairment. They included (i) *General intellectual ability*: Wechsler Test of Adult Reading (WTAR; Wechsler, 2001); the short form of the Wechsler Abbreviated Scale of Intelligence (WASI; Psychological Corporation, 1999). (ii) *Memory tests*: the immediate and delayed Story and Complex Figure recall and List Learning subtests from the Brain Injury Rehabilitation Trust Memory and Information Processing Battery (BMIPB; Coughlan, Oddy, & Crawford, 2007); the Camden Memory Test Short Recognition Memory Test for Words (Warrington, 1996). (iii) *Executive function tests*: the Trail Making Test, FAS letter fluency, and the Colour-Word Interference Test from the Delis-Kaplan Executive Function System (D-KEFS; Delis, Kaplan, & Kramer, 2001).

2.3.2 Experimental Measures

Practice effects were minimised by using two counter-measures (see Belinger, Gaydos, Tangphao-Daniels et al., 2005). Firstly, sleep conditions were counterbalanced across participants. Secondly, alternative forms of each task were used; either published alternatives of standardised tasks, or newly generated alternatives of experimental tasks. For the episodic verbal recall and visual priming lexical decision tasks, two primary word lists were generated from the MRC Psycholinguistic Database, version 2.00 (see Coltheart, 1981), in order to ensure that words were not duplicated across memory tasks. Both sets 1 (episodic recall) and 2

(visual priming) comprised 3 lists of words between four and six letters long which were matched for frequency using the Kucera-Francis written frequency count norms (Frances & Kucera, 1982; Kucera & Francis, 1967). In order to check equivalence of alternative task versions, we compared results across versions administered in the control condition. One way ANOVAs did not find any significant differences across task versions administered for any of the experimental tasks on the control nights.

Computerised tasks were run on a Dell Inspiron laptop computer. Stimuli were generated using Microsoft PowerPoint, and were presented using Superlab Pro version 4.0 software. Responses were made using either designated keys on the integrated keyboard, or an external 2-button Dell mouse.

2.3.2.1 Spatial Span and Spatial Forgetting

Spatial span and spatial forgetting tasks were included to determine whether there were any short-term memory effects, possibly as a result of attentional effects or drowsiness, following sleep deprivation. If there were, these might confound findings on the explicit visuospatial and verbal recall and implicit priming tasks. No specific effect of sleep deprivation was hypothesised for memory consolidation on these two working memory tasks.

Immediate visuospatial memory span was assessed using the Corsi Block test (Milner, 1971), with blocks tapped at a rate of one per second, with two trials administered for each span, matched for difficulty (see Smirni, Villardita, and Zappala, 1983). The

sequence increased in length until an error was made on both trials for a particular span.

The Corsi Blocks were also used in a short-term spatial-span forgetting task. Sequences of four blocks were tapped at a rate of one block per second. Participants reproduced each sequence following a delay of 0, 5, or 15 seconds (counterbalanced across trials). During delays of 5 or 15 seconds, the blocks were covered and participants traced around a set of nine irregularly shaped line-drawings with their finger as quickly as possible, whilst counting backwards in threes from a given two-digit number (see Kopelman, 1991; Sullivan, Corkin, & Growdon, 1986). Two practice trials were performed at each delay interval, followed by five test trials.

2.3.2.2 Episodic Visuospatial Recall Task

Two Spatial Grid tasks (Smith & Milner, 1981) were used. Fifteen line-drawings of common objects placed on a 7 x 7 square grid (A) in a randomised design. Objects on the grid were viewed for one minute, and their locations memorised (cf. Smith & Milner, 1981). The board was covered and, after a two minute distractor interval, participants placed the line drawings (whose order had been shuffled) back in their correct locations on the grid. A second grid (B) with a new set of 15 images was then administered using the same procedure. The following morning, participants were asked to freely recall what the items were and to place them back in position on spatial grid A, followed by spatial grid B.

2.3.2.3 Explicit Verbal Recall Task

The verbal memory recall task assessed factual recall, spatial context memory, and temporal context memory (see Kopelman, Stanhope, & Kingsley, 1997; Rauchs et al., 2004). Two lists (A, B) of 12 nouns were presented; words were presented either towards the top or the bottom of the computer screen in a random order, for five seconds each. To encourage temporal encoding, List A was presented three times, followed by three presentations of List B. Participants were instructed as follows: "Your task is to learn each word, whether the word is in List A or List B, and whether it appears towards the top or bottom of the computer screen; you will be required to recall this information later on." Free recall was tested immediately after the learning of both lists and again the following morning.

2.3.3.4 Visual Priming in a Lexical Decision Task

The priming task comprised a lexical decision task in which participants decided whether a visually presented stimulus represented a 'word' or a 'non-word.' It assessed implicit memory consolidation. In the study phase, 24 nouns, presented serially in the centre of the computer screen, were rated for pleasantness to promote implicit learning (e.g., Graf & Ryan, 1990). An intervening distractor 3-minute line-tracing task was then completed. In the test phase, 24 real nouns (12 studied and 12 new, matched for frequency) and 24 non-words, matched for letter length, were presented in a randomised order for 35 milliseconds each. The stimuli were perceptually degraded using a distortion function in Adobe Photoshop CS4. After each stimulus, participants made a timed lexical decision by pressing the left mouse button to indicate that the stimulus represented a word, and the right button to indicate a non-word.

2.3.3.5 Karolinska Sleepiness Scale (KSS; Akerstedt & Gillberg, 1990)

The KSS measures an individual's subjective sleepiness at a particular time (typically over the preceding 10 minutes). Ratings were obtained between 0 (extremely alert) and 9 (extremely sleepy – fighting sleep), and were used to assess the extent to which concurrent sleepiness affected task performance.

2.3.3.6 Morningness-Eveningness Questionnaire (MEQ; Horn & Ostberg, 1976)

This 19-item scale measured the extent to which an individual tends to prefer completing activities in the morning or the evening. It was included to assess whether morningness-eveningness was related to performance on the tasks following sleep.

2.3.4 Sleep Recording

Polysomnography (PSG) signals were acquired using the Alice 5® Diagnostic Sleep System (Phillips Respironics). A referenced PSG electrode montage was used following the international 10-20 system, with technical specifications in accordance with standardised PSG techniques (Iber, Ancoli Israel, Chesson, & Quan, 2007). Electroencephalographic (EEG) electrodes comprised F2-M1, C3-M2, C4-M1, O2-M1. Left and right electrooculographic (EOG) electrodes were used, and electromyogram (EMG) recordings were acquired from bilateral chin electrodes. Data were acquired in 30-second epochs. SWS was identified if 20% of an epoch showed EEG waveforms depicting slow wave activity. Stages N3 and N4 were scored together as SWS, following the American Academy of Sleep Medicine guidelines (Iber et al., 2007). REM sleep was identified if an epoch comprised low amplitude, mixed frequency EEG in combination with low chin EMG tone and rapid eye movements. PSG recordings were relayed to a computer in the adjacent room via a

network cable so that recordings could be monitored, and electrodes replaced/adjusted (if necessary), by the researchers overnight. Sleep spindles were identified subsequently by a trained scorer within Non-REM sleep (N2 and SWS). Spindles had typical morphology, occurring in the range of 11-16Hz (most commonly 12-14Hz) with duration of at least 0.5 seconds, and were usually maximal in amplitude over central derivations (Iber et al., 2007).

2.4 Procedure

Background neuropsychological testing was conducted 1 to 2 weeks before the sleep study. Participants were asked to maintain their normal sleep pattern in the nights before the sleep studies. Participants reported their adherence to a normal sleep pattern (which included for all participants sleep between the hours of 11pm and 6am at a minimum, to coincide with the experimental schedule), and none were excluded/rescheduled on the basis of their self-report.

Sleep studies occurred over three nights, with a one-week interval between conditions to minimise the interference between the experimental conditions (Van Dongen, Maislin, Mullington, & Dinges, 2003). Each night, participants arrived at the sleep laboratory by 8pm. PSG electrodes were attached and calibrated. From 9pm, experimental tasks were conducted in a fixed sequence, so that fatigue and potential order effects were uniform across tasks and sleep conditions. Testing took approximately one hour. Lights were switched off at 11pm.

On deprivation nights, the sleep stages of interest were visually identified and coded in real-time according to standardised criteria (Iber et al., 2007). Depending on the

sleep condition, either SWS or REM sleep was disrupted; participants were woken from sleep stages and asked to describe an autobiographical memory in response to a stimulus word drawn from a list of common nouns (Crovitz & Schiffman, 1974). Piloting demonstrated that this procedure was more effective in rousing participants from both SWS and REM sleep stages than an auditory tone, and resulted in longer latencies for returning to the sleep stage of interest (cf., Genzel et al., 2009; Weisner et al., 2015 for similar methods). This disruption process was repeated throughout the night to ensure maximal disruption of either SWS or REM sleep. Participants were woken at 6am. In order to minimise possible sleep inertia effects they waited a minimum of 20 minutes before testing. They completed the morning experimental tasks in the same sequence as the evening before (recall and priming without learning). KSS ratings were obtained before and after each evening and morning test session, giving two evening and two morning ratings of subjective sleepiness per sleep condition.

2.5 Analyses

Where data were not normally distributed, transformations (arcsine or logarithmic) were performed before analysis and parametric statics were used (ANOVA). The Wilcoxon Matched-Pairs Test was used to examine differences in the number of disruptions on experimental nights. Pearson's correlations were performed to investigate the relationships between neuropsychological and experimental tests with SWS/REM measures, subjective sleepiness, and spindle counts. Change scores were calculated for experimental measures as a measure of consolidation from night to morning. Data were transformed into Studentised residuals where normative data were not available for experimental tasks. For multiple comparisons, a Sidak

correction (Abdi, 2007) was applied; this correction is similar to the Bonferroni correction but is less conservative, enabling greater retention of statistical power. Similarly, for multiple correlations an adjusted alpha level of .001 was adopted, rather than Bonferroni correction which would require an alpha level of .0008, reflecting an attempt to control for Type I error whilst minimising the likelihood of Type II error. Analyses were run in SPSS, version 20 (SPSS Inc, Chicago IL).

3 RESULTS

3.1 Background Neuropsychological Tests

Table 1 depicts the sample means and standard deviations for each of the neuropsychological tasks administered. Published normative data were used to compute *z*-scores for each test. Participants generally scored above the population means on all measures. Males and females did not differ significantly. We investigated potential relationships between neuropsychological performance, morningness-eveningness scores, and experimental data. No significant correlations were found between any of the variables in the study.

TABLE 1 ABOUT HERE

3.2 Sleep Recording

Manually scored PSG data yielded the total sleep time (total time asleep after sleep onset), SWS, and REM sleep in minutes (see table 2). Differences in total sleep time for the control, SWS, and REM sleep conditions were analysed using a repeated-measures one-way ANOVA; a significant main effect was found [$F(2,32)=9.97$, $p< .001$, $\eta^2_p = .38$]. Pairwise comparisons indicated significantly less total sleep on the SWS deprivation night relative to either the control ($p< .01$) or REM sleep deprivation night ($p< .05$), with no difference in total sleep duration between the control and REM sleep deprivation nights ($p>.05$). However, no significant correlations were found between total sleep time in each sleep condition and performance on any of the experimental tasks.

TABLE 2 ABOUT HERE

The amount of SWS and REM sleep in minutes in each sleep condition was calculated. Data were analysed using a 3 (sleep condition) x 2 (sleep stage duration) repeated-measures ANOVA. There was a significant main effect of both sleep condition [$F(2, 32)=30.01$, $p<.001$, $\eta^2_p = .65$] and sleep stage duration [$F(1,16)=9.67$, $p<.01$, $\eta^2_p = .38$]. There was also a significant interaction [$F(1.29, 20.71)=34.81$, $p<.001$, $\eta^2_p = .69$], such that the 3 experimental conditions had a differential effect on the amount of each sleep stage attained. Compared with the control night, the amounts of SWS and REM sleep differed significantly across the SWS deprivation [$F(1,17)=43.34$, $p<.01$, $\eta^2_p = .73$] and REM sleep deprivation [$F(1,17)=65.04$, $p<.01$, $\eta^2_p = .80$] nights, respectively. Figure 1 shows the mean percentage of REM sleep and SWS obtained on each night. SWS deprivation reduced the amount of SWS by 54%, and REM sleep deprivation reduced the amount of REM sleep by 65%.

FIGURE 1 ABOUT HERE

Although fewer disruptions were required for the deprivation of REM sleep, the mean duration of disruptions was greater. A Wilcoxon Matched Pairs test revealed that the difference between SWS and REM sleep deprivation conditions was significant [T=18, z = -3.73, p<.001, r=.62], such that participants had to be woken more frequently to deprive SWS. However, a paired t-test indicated that the mean duration of disruptions in the SWS condition was significantly shorter than that in the REM sleep condition (t(11)=-2.42, p<.05, r=-.42). Nevertheless, no significant correlations were found between either the number of sleep disruptions or mean duration of disruptions and performance on the experimental tasks.

TABLE 3 ABOUT HERE

3.3 Corsi Span and Corsi Spatial Forgetting Tasks

Table 3 reports descriptive statistics for each of the experimental tasks. In the Corsi span task, although there was a trend towards poorer performance on this task in the morning [F(1,17)=3.91, p=.06, η^2_p =.19], there were no significant differences across sleep conditions [F(2,34)=0.15, p>.05, η^2_p =.01].

The Corsi Spatial Forgetting task data were analysed in terms of a) the number of blocks correctly tapped in the correct sequence, and b) the number of blocks from the sequence that were tapped, regardless of the order in which they were tapped. Night

performance on different nights was consistent across the sleep conditions; hence, the data were averaged to form a single "pre-sleep" condition.

Data were analysed using a 4 (sleep condition) x 3 (delay) repeated-measures ANOVA. There was no effect of sleep condition [$F(1.98,33.69)=1.74$, $p>.05$ $\eta^2_p =.09$]). There was a main effect of delay [$F(2,34)=138.95$, $p<.001$, $\eta^2_p =.89$], with performance on both the 5s [$F(1,17)=134.10$, $p<.001$, $\eta^2_p =.89$] and 15s [$F(1,17)=191.33$, $p<.001$, $\eta^2_p =.91$] delays differing from performance at 0s; pairwise comparisons indicating that performance at both delay intervals was significantly poorer than at 0s (both $p<.001$). There was no interaction effect [$F(6,102)=2.05$, $p>.05$, $\eta^2_p =.11$]. For the random order of recall, there was again a significant main effect for delay interval [$F(2, 34)=107.54$, $p<.001$, $\eta^2_p =.86$], with performance at both the 5s and 15s delays being significantly poorer than that at 0s (pairwise comparisons, both $p<.001$) but neither sleep condition [$F(1.67, 28.38)=.56$, $p>.05$, $\eta^2_p =.03$] nor the interaction effect [$F(3.57, 60.82)=0.46$, $p>.05$, $\eta^2_p =.05$] was significant. Overall, these results indicate that there was no effect of either SWS or REM sleep deprivation on visuospatial short-term forgetting, relative to the control condition.

3.4 Spatial Grid Task

First, free recall of the objects from the spatial grids was analysed, to see whether memory for the objects themselves was affected by SWS deprivation. One-way ANOVAs indicated that there was no difference in memory recall across sleep conditions for either grid A [$F(2, 32)=.35$, $p>.05$, $\eta^2_p =.02$] or grid B [$F(2, 32)=1.63$, $p>.05$, $\eta^2_p =.09$].

Figure 2 shows difference scores between evening and morning performance for displacement errors for spatial grid A. Performance was worse in the morning in all conditions. It can be seen that the displacement errors were virtually identical between the control and the REM-disrupted night, but much larger after slow wave disrupted night. On statistical analysis, there was a highly significant effect of test time [$F(1,16)=38.69$, $p<.001$, $\eta^2_p=.71$]. The main effect of sleep condition was not statistically significant [$F(2,32)=.11$, $p>.05$, $\eta^2_p=.01$]. Importantly, the test time by sleep condition interaction was statistically significant [$F(2,34)=4.47$, $p<0.05$, $\eta^2_p=.22$], and the contrast for this interaction between the control and slow wave conditions, taken in isolation, was also significant [$F(1,16)=4.67$, $p<0.05$, $\eta^2_p=.23$]. The overall interaction effect across the three conditions was also significant when scores were expressed as a percentage of the total displacement error as per the Smith et al. (1995) scoring procedure [$F(2,34)=3.97$, $p<0.05$, $\eta^2_p=.19$], and after arcsine correction [$F(2,34)=4.41$, $p<0.05$, $\eta^2_p=.22$]. However, when spatial grid B was administered, this time of day by sleep condition interaction effect disappeared [$F(2,32)=0.19$, $p>.05$, $\eta^2_p=.01$].

FIGURE 2 ABOUT HERE

3.5 Explicit Verbal Recall Task

The percentage of correctly recalled words was calculated. Spatial and temporal findings were analysed only for correctly recalled words. Relative to pre-sleep and control performance, morning scores were reduced following both SWS and REM deprivation in terms of both correct recall and spatial position (Figure 3). Performance in the SWS and REM sleep deprivation conditions was compared with

the mean of the pre-sleep and control performance. A 4 (sleep condition) x 2 (memory task) repeated-measures ANOVA was conducted. There was a significant main effect of sleep condition [$F(2.02, 34.34)=6.02$, $p<.01$, $\eta^2_p = .26$]. Contrasts indicated significant differences in performance relative to pre-sleep for both SWS [$F(1,17)=19.16$, $p<.001$, $\eta^2_p = .53$], and REM sleep [$F(1,17)=18.52$, $p<.001$, $\eta^2_p = .52$], but not for undisturbed control sleep [$F(1,17)=1.23$, $p>.05$, $\eta^2_p =.07$]. There was also a main effect of memory task; word recall was significantly greater than recall of spatial position [$F(1,17)=9.39$, $p<.01$, $\eta^2_p = .36$]. However, there was no significant interaction [$F(1.31, 22.27) = .59$, $p>.05$, $\eta^2_p =.03$]. Overall, this task indicated that both SWS and REM deprivation had a negative effect on the recall of factual (word) and spatial information.

FIGURE 3 ABOUT HERE

For temporal information, morning performance was generally poorer than pre-sleep performance across all sleep conditions. A 3 (sleep deprivation condition) x 2 (test time) repeated-measures ANOVA revealed a significant main effect of time of day [$F(1,17)=45.08$, $p<.01$, $\eta^2_p = .73$], and no effect of sleep deprivation [$F(2,34)=2.08$, $p>.05$, $\eta^2_p =.11$]. All groups performed worse in the mornings than at night, but there was no specific effect of sleep deprivation on the recall of temporal information.

To test whether there were any first night or practice effects, the data were reordered according to task version/run order. A one-way, repeated-measures ANOVA of word recall did not reveal any significant differences [$F(2.34) = 3.16$, $p>.05$, $\eta^2_p =.16$].

Therefore, the observed findings were not attributable to either first night or practice effects.

3.6 Visual Priming in a Lexical Decision Task

Response accuracy and latencies were calculated for each of the three types of stimuli (primed, unprimed, and non-word stimuli). Successful priming was indicated where lexical decision latencies were significantly faster, and accuracy significantly greater, for primed stimuli than for unprimed stimuli or non-words. As there were no differences across conditions, night data were collapsed into a single pre-sleep condition.

Accuracy for words was superior to that for non-words and there was a clear priming effect in the pre-sleep condition, but not in any of the morning conditions. A 4 (sleep condition) x 3 (stimulus type: non-word, unprimed, primed) repeated measures ANOVA indicated that there was a main effect of stimulus type [$F(1.24, 20.99)=3.94$, $p<.05$, $\eta^2_p = .19$]; performance for primed words was significantly better than that for non-words [$F(1,17)=4.66$, $p<.05$, $\eta^2_p = .22$], but not unprimed words [$F(1,17)=3.79$, $p>.05$, $\eta^2_p =.18$]. However, there was no significant effect of sleep condition [$F(3,51)=0.74$, $p>.05$, $\eta^2_p =.04$], nor any significant sleep condition by stimulus type interaction [$F(3.33, 56.54)=2.35$, $p>.05$, $\eta^2_p =.12$].

For mean latencies, there was a priming effect in the pre-sleep condition, but not in any of the morning conditions. Log-transformed data were analysed using a 4 (sleep condition) x 3 (word type) repeated-measures ANOVA. No effect of sleep condition was found [$F(1.56, 26.52)=0.12$, $p>.05$], but there was a significant main effect of

stimulus type [$F(2, 34)=15.00$, $p<.001$, partial $\eta^2 = .47$]. Latencies for non-word stimuli were significantly longer than those for primed stimuli [$F(1,17)=18.87$, $p<.001$, partial $\eta^2 = .53$]. There was also a significant interaction between sleep condition and stimulus type [$F(6, 102)=2.75$, $p<.05$, $\eta^2_p = .14$]. The prolonged latencies for non-words and unprimed words (relative to primed words) in the pre-sleep condition were eliminated in the morning conditions.

We calculated *A′* (cf., Zhang & Muller, 2005) for the accuracy data from the hit-rate and false-alarm rate. One-sample t-tests showed that performance in all sleep deprivation conditions was found to be significantly better than chance: control morning [$T(17)=11.34$, $p<.05$, $r=.88$], SWS morning [$T(17)=6.71$, $p<.05$, $r=.75$], REM sleep morning [$T(17)=8.75$, $p<.05$, $r=.82$]. Participants were able to discriminate accurately between words and non-words at a level significantly better than chance. A Friedman's ANOVA did not yield significant differences among sleep conditions for either pre-sleep [χ^2 (2)=3.80, $p>.05$] or morning [χ^2 (2)=0.89, $p>.05$] tasks.

3.7 Subjective Sleepiness

There were no significant differences in performance across night conditions; therefore, data were averaged into a single pre-sleep condition. Because a non-parametric test would not be able to analyse any interactions, a 4 (sleep condition) x 2 (KSS order: pre-test, post-test) repeated-measures ANOVA was conducted as an exploratory measure. A significant main effect of sleep condition was found [$F(3,51) = 4.65$, $p< .01$, $\eta^2_p = .22$], with overall sleepiness in the SWS condition being significantly different from that in the pre-sleep condition [$F(1,17) = 22.5$, $p< .01$, η^2_p

= .57]. Pairwise comparisons indicated that sleepiness in the SWS morning condition was greater than that in the pre-sleep condition (p<.001). However, importantly, there were no significant differences in morning sleepiness across the experimental conditions (p>.05). There was no significant main effect of KSS (before/after testing) sequence [$F(1,17) = 0.06$, $p > .05$, $\eta^2_p = .004$]. There was a significant sleep condition x KSS sequence interaction [$F(3,51) = 7.41$, $p < .001$, $\eta^2_p = .30$], indicating that sleepiness increased between pre- and post-test KSS ratings in the pre-sleep conditions, but decreased (i.e., alertness increased) between pre- and post-test KSS ratings across the morning conditions.

Pearson correlations indicated that there was no significant relationship between the amount of SWS or REM sleep obtained on any of the three sleep nights and the KSS ratings obtained on the following mornings. More specifically, we examined whether the amount of SWS and REM sleep in minutes was related to performance on experimental tasks. None of the correlations were significant at the adjusted alpha level of .001. Neither were there any significant correlations between sleepiness (pre- and post-test KSS ratings) and either night or morning performance on any of the experimental tasks.

3.8 Spindle Analysis

Finally, we carried out a post-hoc analysis of the relationship between spindle count and task performance. Data from one participant was omitted from analyses because of polysomnography trace artefacts. A one-way ANOVA showed a significant main effect of sleep condition [$F(2,28)=4.23$, $p<.05$, $\eta^2_p = .23$]. Contrasts indicated that, when compared with the control night, significantly fewer spindles occurred on the

SWS deprivation night [$F(1,14)=8.11$, $p<.01$, $\eta^2_p = .37$] than on the REM sleep deprivation night [$F(1,14)=0.05$, $p>.05$, $\eta^2_p = .003$]. There was no significant difference between the control and REM-deprived nights ($p>.05$). There were no significant correlations between spindle count and any of the task change scores.

4 DISCUSSION

In this study, we selectively deprived SWS or REM sleep over the entire night to examine the effects on the consolidation of explicit and implicit memories. Importantly, our design permitted the precise identification of when a participant entered SWS or REM sleep, and recording of the total overnight SWS and REM durations. The level of sleep deprivation achieved in this study was similar to that obtained for SWS and REM sleep in previous studies using split-night deprivation designs (e.g., Gais et al., 2000; Plihal & Born, 1999; Rauchs et al., 2006); and the amount of REM sleep reduction was similar to that in another study using a selective deprivation design (Saxvig et al., 2008). By depriving either SWS or REM sleep throughout the night, and carefully recording their respective durations, we were able to be more confident of 'pure' SWS/REM sleep deprivation than is possible using a split-night design. Consequently, it is reasonable to assume that observed decrements in performance following the experimental nights were attributable to the selective deprivation of either SWS or REM sleep, respectively.

4.1 Pattern of Findings on Explicit Memory Tests

On the Corsi Span and Corsi forgetting tasks, there was no specific effect of either SWS or REM sleep deprivation with respect to visuospatial working memory. This

suggests that deprivation did not lead to attentional effects on these working memory tasks, and attentional effects were unlikely to have confounded performance on the other memory tasks.

By contrast, on the Spatial Grid task, we found that delayed recall of visuospatial position was selectively affected by SWS deprivation for Grid A, consistent with spatial memory studies in animals (e.g., Palvides & Wilson, 1989; Wilson & McNaughton, 1994). Object recall was not significantly affected by SWS or REM sleep disruption, indicating that the effect of SWS deprivation was specific to memory for visuospatial contextual information. The latter finding is consistent with theories that hippocampal function is central to the binding of complex associations or the relations between items (Mayes and Downes, 1997; Eichenbaum, 2001; Monti, Cooke, Watson, et al., 2014), and suggests that SWS is necessary for this aspect of memory consolidation. This effect was not replicated for Grid B, which may reflect a proactive interference effect from Grid A.

On the verbal free recall task, it was clear that both SWS and REM sleep deprivation had a negative effect on the recall of words and spatial locations, and a full night of sleep yielded optimal performance. There was no significant difference between the effects of SWS and REM sleep deprivation. We did not obtain a significant effect on memory for temporal context, although this has been reported in some previous investigations (Drosopoulos, Windau, Wagner, & Born, 2007; Harrison & Horne, 2000; Rauchs et al., 2004).

In terms of our first hypothesis, therefore, the consolidation of explicit memories was more consistently related to disruption of SWS, but disruption of REM also affected performance on the verbal recall task.

4.2 Implicit Memory Findings

On our implicit verbal memory task, priming was demonstrated on the evening task before sleep (cf., Tulving & Schacter, 1990), but this priming effect did not carry over to the morning for any of the sleep conditions, for either accuracy or response latencies. Thus, our second hypothesis was not supported; and this result contrasts with the significant effects of SWS deprivation on explicit spatial and verbal memory, and REM sleep deprivation on explicit verbal recall. Some, but not all, previous studies have suggested that sleep may play a role in the transformation of implicitly encoded information into explicit representations (Fischer, Drosopoulos, Isen, & Born, 2006; Genzel et al., 2009; Rauchs et al, 2006; Yordanova, Kolev, Verleger et al., 2008) . Stickgold, Whidbee, Schirmer, Patel & Hobson (2000) have suggested that most REM sleep occurs in the last quartile of sleep, and other studies have suggested that consolidation of implicit memories is dose-dependent, with more sleep conferring greater benefit (Dieklemann et al., 2009). The wake-up time was 6am in this study, potentially meaning that participants missed an episode of REM sleep. This may have prevented full implicit memory consolidation in the control condition, obscuring potential deprivation effects. Mednick et al. (2003) have suggested that short naps of 60-90 minutes improve performance, provided both SWS and REM sleep occur within that time. Indeed, Mednick et al., 2003 obtained a magnitude of effect from short naps on a visual texture discrimination task comparable to that seen in an overnight study (Stickgold et al,2000). Consequently, the reduced REM sleep

window in the present perceptual memory task, should have been sufficient to identify any implicit memory effect in the control condition. However, equally this could mean that a small amount of REM sleep obtained in the REM sleep deprivation condition may have potentially obscured a deprivation effect in this instance. Given the early wake up time, the extent to which the role of REM sleep in implicit memory can be assessed is somewhat limited. However, we did obtain a significant REM sleep deprivation effect in the episodic memory task, and there were no significant correlations between either the amount of REM sleep or REM sleep deprivation and performance on any of the experimental tasks.

4.3 Subjective Sleepiness

Subjective measures of sleepiness indicated that, generally, participants became sleepier over the course of night testing and more alert over the course of morning testing. This is in line with what might be expected on the basis of circadian influences and sleep homeostasis (Van Dongen & Dinges, 2000). Sleepiness had the potential to exaggerate the difference in performance between night and morning tasks, which might have confounded findings on the memory tasks. However, we found that sleepiness was not related to the amount of either SWS or REM sleep on any of the three sleep nights. Moreover, there was no significant relationship between sleepiness and either pre-sleep or morning performance on any of the experimental tasks in any of the sleep conditions.

Given the absence of any correlation with the sleepiness data, the specific pattern of findings on episodic visuospatial and verbal memory in our study are very unlikely to have resulted from general fatigue or reduced alertness, rather than the specific effects

of SWS and REM disruption on memory consolidation. Moreover, we did not find any significant relationship between circadian preference (morningness-eveningness) and performance on the experimental tasks.

4.4 Spindle Count

Some previous studies have found a relationship between spindle density and memory consolidation (e.g., Bakarat et al., 2011; Bodizs et al., 2008; Genzel et al., 2009; Mednick et al., 2013; Morin, Doyon, Dostie et al., 2008; Schabus et al., 2004). We did not find significant correlations between spindle counts and any of our experimental variables, following correction for multiple comparisons. Consistent with this, Tamminen, Payne, Stickgold et al. (2010) failed to find any correlations between spindle counts and overnight novel word recall or recognition memory. Their data suggested that spindles were less important in strengthening explicit recall than SWS. Given that we conducted only a limited examination of spindle count, this would benefit from further exploration in future studies.

4.5 Theoretical Implications

Recent studies employing other techniques of sleep manipulation (e.g., transcranial oscillation induction and pharmacological manipulation) have provided further support to the association between SWS and explicit memory consolidation. By contrast, the contribution of REM sleep has sometimes been attributed to a stabilisation of consolidated memories or, alternatively, to a specific role in perceptual or implicit memory (Ackermann and Rasch 2014; Mednick et al 2013; Rasch and Born 2013). Spindle density has been variously linked to episodic memory consolidation, implicit memory, or to neither (Mednick et al 2013; Tamminen et al,

2010; Westerberg et al, 2012). In the present study, using a sleep deprivation technique combined with detailed recordings of each sleep stage, we obtained further evidence for the contribution of SWS in explicit verbal and spatial episodic memory, but not in tasks relying on attention or working memory. On our verbal memory task, but not on our spatial or implicit memory tasks, we also found a significant effect of REM sleep.

Our findings can be considered in terms of the dual-process, sequential, and active systems consolidation hypotheses of memory consolidation outlined in the Introduction. The finding of a role for both SWS and REM sleep in our verbal memory task may simply reflect an additive effect; however, the results also suggest that a full night of sleep, comprising a cyclical succession of sleep stages, optimises overnight memory consolidation of information in this explicit task (Diekelmann & Born, 2010; Gais et al., 2000; Giuditta et al., 1995; Inostroza & Born, 2013; Landmann et al., 2014; Stickgold, 2009; Stickgold & Walker, 2007; Walker & Stickgold, 2010). On this task, the results were consistent with the sequential hypothesis that sleep stage specificity exists, not for categories of memories, but for stages in the consolidation process (Stickgold, 2009), that is, that there are sequential stages in memory consolidation and stabilisation. Morning performance in our verbal memory task benefitted from the occurrence of both SWS and REM sleep in a cyclical fashion over the course of the night; and performance was impaired when either SWS or REM was reduced New learning in this task may also have been subject to active system consolidation (e.g., Born & Wilhelm, 2012) that required SWS to drive repeated reactivations of the newly encoded memory for initial consolidation from the short term into the long term memory store, and REM sleep

for stabilisation of that memory representation. Whilst our behavioural findings are consistent with both hypotheses, it is difficult to conclude definitively whether the sequential hypothesis or the active system consolidation hypothesis is the more appropriate model of memory consolidation without further study. However, given that consolidation was optimised by a full night of sleep, rather than depending solely on processes peculiar to a specific sleep stage, our findings suggest that the dual-process hypothesis appears inadequate in capturing the role of sleep in memory consolidation in this task (cf., Akermann & Rasch, 2014; Stickgold, 2013).

4.6 Potential Limitations

Participants were young, healthy, well-educated individuals and may have been more resistant to the effects of selective sleep deprivation than others in the population. Additionally, it could be argued that the selective sleep deprivation method used does not reflect naturally occurring selective sleep deprivation in some individuals due to underlying brain dysfunction, which may disrupt memory consolidation for reasons beyond simply the loss of SWS or REM sleep. Nevertheless, in our sample, using a selective sleep deprivation protocol, we found that SWS deprivation affected the consolidation of memory for spatial locations, and that both SWS and REM sleep deprivation affected verbal episodic memory. These findings provide a starting point at least in understanding memory consolidation during sleep.

Participants were asked to keep their normal sleep pattern in the week before the study nights and adherence was checked by self-report. It could be argued that self-report confirmation is unreliable. However, actigraphy, which is often used to examine pre-study sleep patterns, is also problematic as it measures movement rather

than sleep. Actigraphy can over-estimate sleep rate and efficiency, and it is poor at identifying wakefulness (Chae et al., 2009; Pollak et al., 2001; Sadeh, 2011; Tyron, 2004). For this reason, not all published reports have used actigraphy (e.g., Wiesner et al. 2015). Similarly we have not used actigraphy and acknowledge that a reliance on self-report may represent a less reliable way of assessing adherence to the pre-study sleep schedule. It is possible that a relatively low total sleep time (minimum 7 hours) leading up to the study may have affected sleep stages during the control night for some participants and we aimed to minimise these effects by counterbalancing sleep conditions across participants.

Stickgold et al. (2000) suggested that 6 hours of sleep is a 'golden figure' for consolidation to occur. In this study, the mean total sleep time was 6.13 hours on the control night. On the episodic memory task, for example, performance on the morning following the control night did not differ significantly from night-time performance. However, following both REM sleep and SWS deprivation, performance on words and spatial locations differed significantly from night-time performance. This suggests that deterioration was observable on the experimental nights in this task. However, it could be argued that 6 hours of sleep might not necessarily be a 'golden figure' for all types of memory consolidation. The possibility exists that 6 hours of sleep on the control night may not have been sufficient in all tasks (e.g., the implicit memory task), giving rise to a floor effect which might have obscured potential SWS or REM sleep deprivation effects.

Although we successfully deprived a significant amount of both SWS and REM sleep, comparable with deprivation levels in split-night studies, it could be argued that a

sufficient amount of each sleep stage was present to obscure potential deprivation effects on memory consolidation in some tasks. Participants permitted to have a nap immediately after learning show benefit, relative to those who do not, on both explicit and implicit memory tasks (e.g., Backhaus & Junghanns, 2006; Lahl, Wispel, Willignes, & Pietrowsky, 2008; Mednick, et al., 2003; 2013). However, given the specific pattern of effects we obtained, it is reasonable to conclude that, in our study, SWS deprivation disrupted the consolidation of visuospatial information, and that the disruption of both SWS and REM impaired the consolidation of verbal episodic memories.

Although significantly more disruptions were required during the deprivation of SWS than during the deprivation of REM sleep, leading to a reduced total sleep time on the SWS night, this may have reflected the fact that there was proportionally more SWS than REM sleep during the control night. Moreover, we did not find any significant correlations between the number of awakenings (i.e., deprivation) and task performance.

In identifying REM sleep, we adhered to the AASM criteria (Iber et al., 2007) and therefore it is possible that tonic REM sleep, in which eye movements are absent (Carskadon & Dement, 1989), was not effectively deprived. Nevertheless, there was a clear effect of REM sleep deprivation on the episodic verbal recall task.

4.7 Summary and Conclusions

Overall, our behavioural findings suggested that the role of sleep in memory consolidation varied for different types of information. An implicit lexical decision

task and tasks measuring attentional and working memory processes appeared to be unaffected by the deprivation of either SWS or REM sleep. SWS deprivation affected the consolidation of memory for spatial locations, a finding consistent with split-night studies. Both SWS and REM sleep deprivation affected verbal episodic memory.

Interestingly, the pattern of performance on the different types of memory task in our study echoes the pattern of performance found in neurological and drug-induced amnesia, where typically explicit memory is impaired in the context of spared working and implicit memory (Curran, Schifano & Lader, 1991; Deweer, Ergis, Fossati, et al., 1994; Kopelman, 2002; Kopelman & Corn, 1988; Mayes, 1988; Squire and Schacter, 2002).

In conclusion, we found that, where the sleep cycles were measured across the night, neither SWS nor REM sleep deprivation affected aspects of short-term or working memory, nor a measure of implicit memory. By contrast, SWS deprivation had a disruptive effect on the consolidation of explicit memories for visuospatial location; and both SWS and REM sleep deprivation adversely affected explicit verbal recall. Spindle count was not correlated with either explicit or implicit memory performance. These findings demonstrate the need to measure sleep cycles throughout the night. Taken together, they provide evidence for the importance of both SWS and REM sleep in the overnight memory consolidation of explicit memories.

5 ACKNOWLEDGEMENTS

This research was funded by research monies from the Psychiatry Research Trust at the Institute of Psychiatry, Psychology and Neurcience, and by research funding

contributed by Dr Irshaad Ebrahim at the London Sleep Centre. MDK and LHG receive salary support from the National Institute for Health Research (NIHR) Dementia Biomedical Research Unit at the South London and Maudsley NHS Foundation Trust and King's College London. The views expressed are those of the authors and not necessarily those of the NHS, the NIHR, or the Department of Health.

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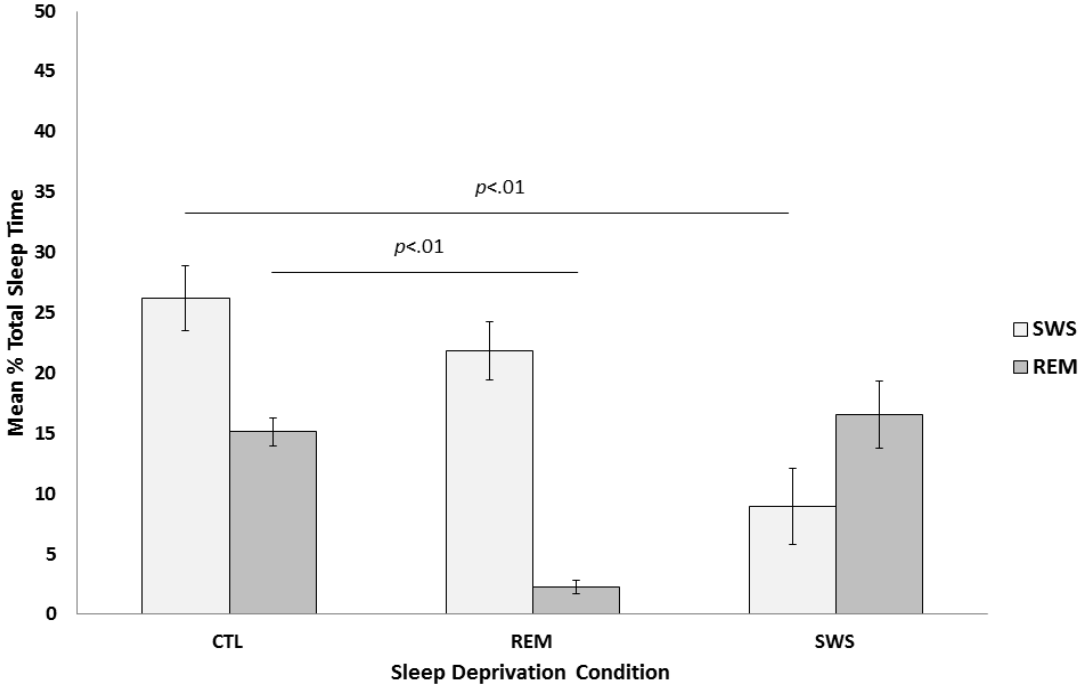

Figure 1. Mean percentage of REM and SWS obtained on each sleep night.

Error bars represent ± 1 standard error of the mean (SEM).

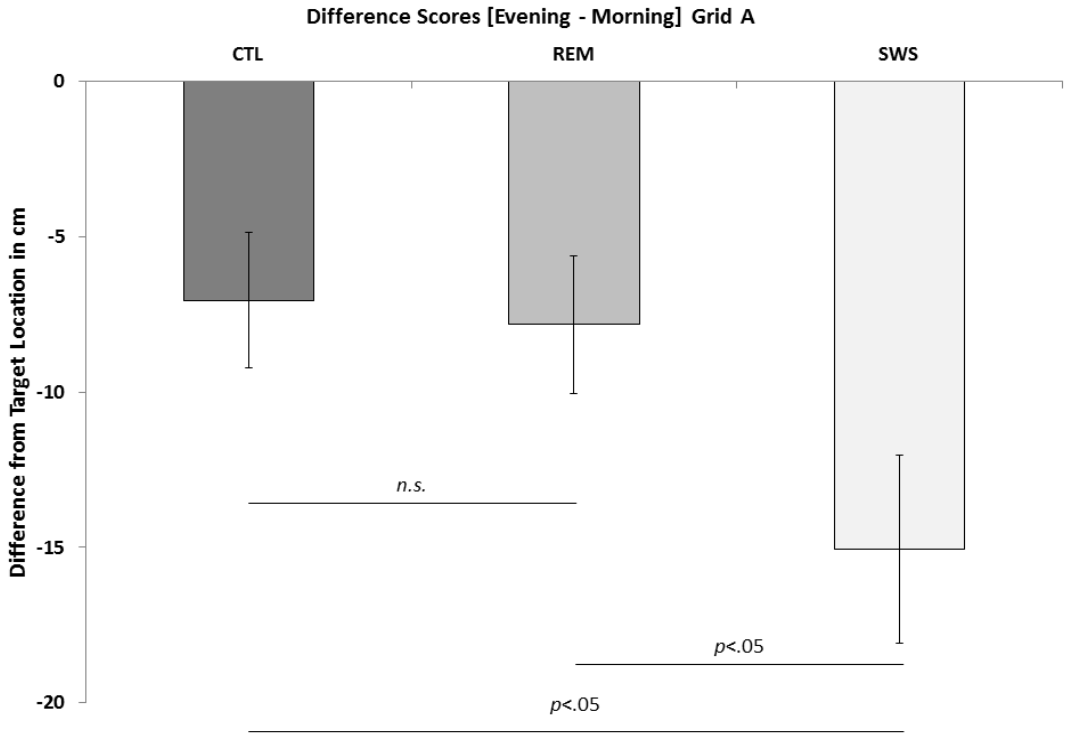

Figure 2. Displacement error on Spatial Grid A shown as the distance of the object from the target location in centimetres.

Error bars represent ± 1 SEM.

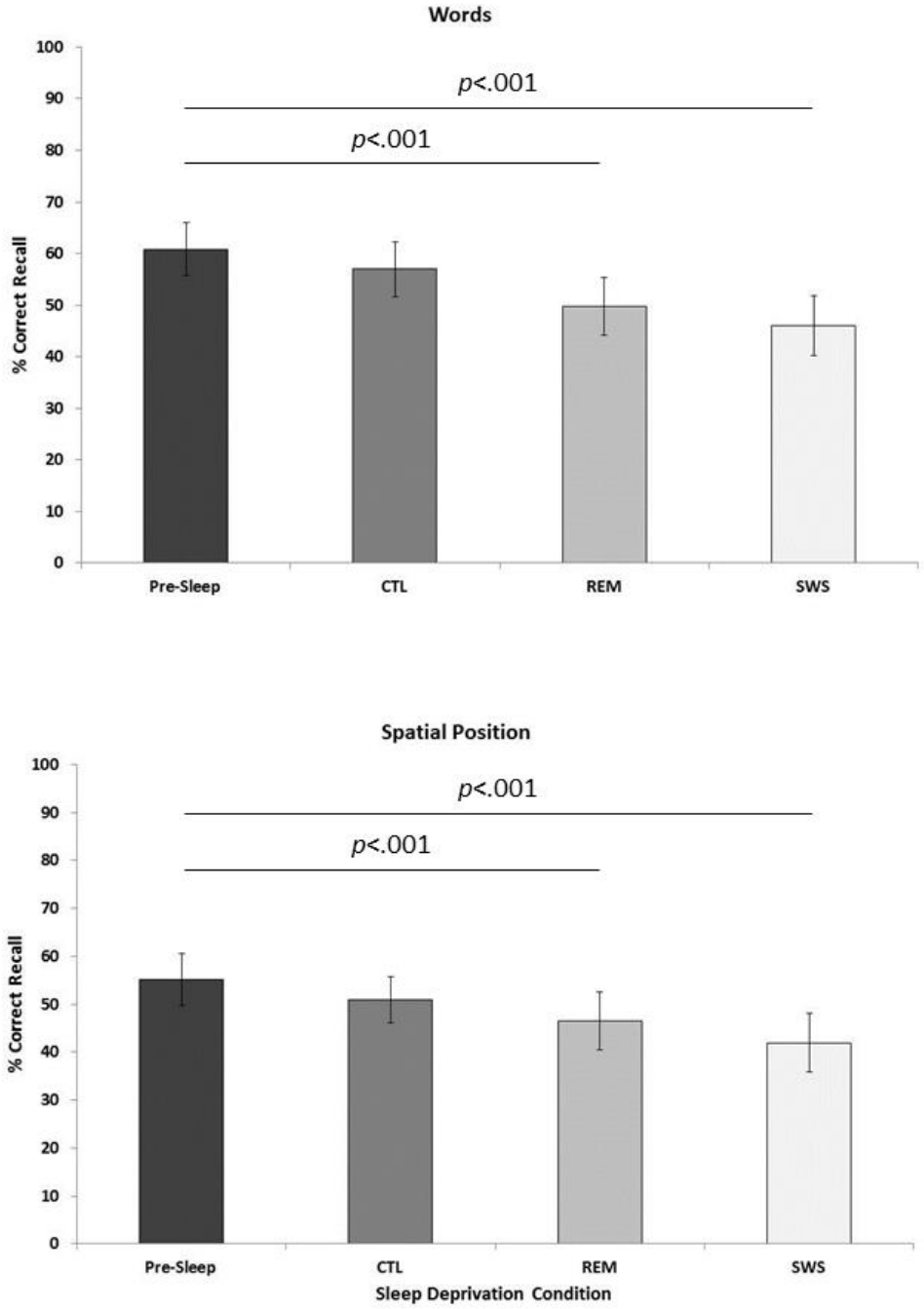

Figure 3. Mean percentage correct responses for words and spatial positions in the list learning task.

The pre-sleep condition represents the mean pre-sleep performance across the three conditions. Remaining bars represent the performance on morning tasks following control (non-deprived) sleep or selective SWS or REM sleep deprivation. Error bars represent ± 1 SEM.

Table 1. Cognitive screening data.

Means and Standard Deviations represent those of the sample. LL= Lower Limit, UL = Upper Limit.

Neuropsychological Test	**Results**				
				95% CI	
	M	*SD*	*z*-score	LL	UL
WTAR (predicted Full Scale IQ)	110.39	4.12	0.69	0.57	0.82
WASI					
2 subtest Full Scale IQ	121.11	5.89	0.90	0.02	1.78
BMIPB					
Stories					
Immediate	30.5	5.76	0.23	-0.04	0.50
Delayed	30.5	6.82	0.48	0.16	0.80
Word List					
Learning	62.39	7.03	0.60	0.26	0.94
Delayed	13.39	1.72	0.49	0.20	0.78
Figure					
% Immediate	81.72	9.62	0.13	-0.31	0.57
% Delayed	81.85	8.62	0.60	0.25	0.94
% Retained	100.20	5.96	0.69	0.41	0.97
Camden Short Recognition Memory Test for Words	25	0	0.81	-	
D-KEFS					
Letter Fluency Scaled Score	13.83	2.62	1.28	0.87	1.68
Trail Making Test Number-Letter Switching Scaled Score	11.67	2.66	0.35	-0.24	0.94
Colour-Word Interference					
Inhibition Scaled Score	12.33	2.91	0.78	0.33	1.23
Inhibition-Switching Scaled Score	11.78	1.77	0.59	0.32	0.86

Table 2. Polysomnography data.

Measure	Mean (SD)		
	CTL	**REM**	**SWS**
Total Sleep Time[a]	367.5 (14.1)	359.9 (14.6)	287.7 (18.7)
Sleep Duration[a]			
REM Sleep	57.1 (20.4)	6.59 (4.9)	48.3 (43.4)
SWS	90.2 (36.9)	74.1 (38.1)	13.8 (10.8)
Number of Disruptions[b]	-	12.7 (19.4)	37.2 (5.9)
Duration of Disruptions[a]	-	7.9 (4.9)	4.3 (25)
Spindles[b]	330.7 (151.6)	246.5 (186.8)	344.8 (268.1)

[a] time in minutes; [b] count

Table 3. Descriptive statistics for the experimental tasks.

Measure	Mean (SEM)			
	Pre-Sleep	**CTL**	**REM**	**SWS**
Corsi Span Task[a]				
Evening	-	71.6 (3.1)	70.4 (1.8)	71.6 (1.9)
Morning	-	68.6 (2.2)	67.9 (2.0)	68.5 (1.9)
Corsi Forgetting Task[b]				
Correct				
0	1.51 (0.04)	1.3 (0.03)	1.15 (0.03)	1.27 (0.03)
5	1.47 (0.08)	1.49 (0.10)	1.18 (0.15)	1.18 (0.14)
15	1.43 (0.08)	1.4 (0.12)	1.5 (0.16)	1.14 (0.12)
Random				
0	1.92 (0.01)	3.14 (0.01)	1.15 (0.02)	1.2 (0.01)
5	1.91 (0.06)	2.4 (0.09)	2.2 (0.11)	2.3 (0.10)
15	2.2 (0.06)	2.1 (0.11)	2.1 (0.11)	2.0 (0.07)
Spatial Grid Task				
Object Recall A[c]	-	5.5 (0.61)	5.2 (0.45)	5.4 (0.66)
Object Recall B[c]	-	8.2 (0.91)	7.0 (0.50)	7.3 (0.65)
Grid A[d]				
Difference	-	-7.01 (2.2)	-7.8 (2.2)	-15.1 (3.0)*
Grid B[d]				
Difference	-	-6.4 (1.8)	-4.8 (1.9)	-5.5 (1.8)
Episodic Verbal Recall[a]				
Words				
	60.8 (4.26)	56.9 (5.34)	49.76 (5.7)*****	46.06 (5.8)*****
Spatial Location				
	55.1 (4.76)	50.9 (4.75)	46.5 (5.9)*****	41.9 (6.2)*****
Temporal List				
Evening	-	66.9 (5.03)	58.8 (5.5)	53.9 (5.3)
Morning	-	49.3 (6.6)	47.2 (5.8)	43.8 (5.9)
Visual Priming in a Lexical Decision Task				
Accuracy[b]				
Non-words	1.53 (0.03)	1.49 (0.06)	1.46 (0.05)	1.45 (0.04)
Unprimed	1.52 (0.03)	1.66 (0.06)	1.64 (0.07)	1.64 (0.05)
Primed	1.72 (0.03)	1.63 (0.07)	1.58 (0.05)	1.60 (0.05)
Latencies[e]				
Non-words	7.30 (0.04)	7.27 (0.04)	7.29 (0.06)	7.25 (0.08)
Unprimed	7.25 (0.04)	7.17 (0.04)	7.22 (0.05)	7.27 (0.05)
Primed	7.19 (0.04)	7.19 (0.04)	7.25 (0.06)	7.240.05)

a. percent correct; b. radians; c. number; d. distance from target in centimetres; e. natural log

***** sleep deprivation effect